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LOCAL APPROXIMATION OF A METAPOPULATION'S EQUILIBRIUM

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ABSTRACT. We consider the approximation of the equilibrium of a metapopulation model, in which a finite number of patches are randomly distributed over a finite subset Ω of Euclidean space. The approximation is good when a large number of patches contribute to the colonization pressure on any given unoccupied patch, and when the quality of the patches varies little over the length scale determined by the colonization radius. If this is the case, the equilibrium probability of a patch at z being occupied is shown to be close to $q_1(z)$, the equilibrium occupation probability in Levins's model, at any point $z \in \Omega$ not too close to the boundary, if the local colonization pressure and extinction rates appropriate to z are assumed. The approximation is justified by giving explicit upper and lower bounds for the occupation probabilities, expressed in terms of the model parameters. Since the patches are distributed randomly, the occupation probabilities are also random, and we complement our bounds with explicit bounds on the probability that they are satisfied at all patches simultaneously.

Keywords: incidence function model, spatially realistic Levins model

MSC 2010: 92D40; 60J10; 60J27

1. Introduction

A number of papers have addressed the problem of approximating a complex metapopulation model by Levins's model [5, 9, 3, 12, among others]. For example, in the setting of Ovaskainen and Cornell [12], a metapopulation is taken to consist of an infinite number of patches in $\mathbb{R}^d$. In their simplest case, the locations of the patches are determined by

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a Poisson point process with constant intensity measure; they also consider stationary point processes with spatial correlation. The colonization rate of an empty patch is determined by its distance from the occupied patches and by a colonization kernel. Under such conditions, Ovaskainen and Cornell [12] give asymptotic expansions describing the differences between the equilibrium properties of the metapopulation and what would be expected under a uniform mean field Levins model, in the limit where the range of the colonization kernel tends to infinity. Their expansions were formally justified in [13].

In this paper, we take a somewhat different approach. First, we are interested in metapopulations which are not infinite in extent, but consist of only finitely many patches, and whose underlying landscape is not uniform; in particular, it might consist of a number of regions in which the metapopulation is viable, separated by regions where it is not. In previous work [2], we have demonstrated that deterministic metapopulation models provide good approximations to their stochastic counterparts, at least over finite time horizons, provided that the colonization pressure at a patch results from the sum of the effects of many other patches — this is equivalent to the assumption in Ovaskainen and Cornell [12] that the colonization kernel has long range. However, if the landscape is not uniform, even the equilibrium state of the deterministic system is unknown. In this paper, we show how to construct an approximation to the equilibrium state of the deterministic system, provided that the properties of the landscape do not vary much over the range of the colonization kernel. The approximation is local, in the sense that the equilibrium probability of a patch at position z being occupied is what it would be if the landscape were everywhere constant, with its parameters taking the values that are taken at z. Rather than justifying the approximation in terms of limit theorems, we prefer to give explicit bounds on the accuracy of the approximation, which depend on the expected number of patches contributing to the colonization pressure at a given patch, on the possible variation of the landscape within the colonization radius, and on the ratio of the colonization radius to the diameter of the entire region — in a finite region, boundary effects also play a part. Patches are modelled as the points of a Bernoulli point process with spatially varying intensity, and so such error bounds cannot be definitive; instead, we also give expressions bounding the probability that our error bounds are correct.

2. The equilibrium of a metapopulation

The incidence function model of Hanski [6] in d dimensions for a metapopulation comprising n patches spread over a habitat Ω of volume A is a discrete time Markov chain on $\mathcal{X} := \{0,1\}^n$. Usually, $d = 2$, and we think of volume as an area, but this is not needed here. Denote this Markov chain by $X_t = (X_{1,t}, \ldots, X_{n,t})$, where $X_{i,t} = 1$ if patch i is occupied at time t and $X_{i,t} = 0$ otherwise. We assume that the patch size and its ability to support a local population depend only on the patch location. Let $z_i \in \Omega \subset \mathbb{R}^d$ denote the location of the i-th patch. The transition probabilities of the Markov chain are determined by how well the patches are connected to each other and by the probability of local extinction. Define the functions $S_i \colon [0,1]^n \mapsto [0,\infty)$, which represent the aggregate migration pressure on patch i from the remaining patches, by

$$S_i(x) \;=\; \frac{A}{(n-1)} \sum_{j \neq i} a(z_j) c(z_i, z_j; r) x_j, \tag{2.1}$$

where

$$c(z, y; r) \;:=\; r^{-d} c_z(\|z - y\|/r),$$

and, for each z, c_z is an integrable function with maximum value at most $c_{\max}$. In what follows, we assume that $c(x) = 0$ for $x > 1$, so that the migration range is bounded by r; this is to simplify the analysis, and could be relaxed. The average density of population is given by the ratio n/A, so that, within such a range, there can be expected to be about nr^d/A patches, over which the migration effort of a patch j is distributed. Hence each patch contributes about $(nr^d/A)^{-1}$ of its effort to each other neighbouring patch, and this is why the ratio $A/(n-1)$ appears in S_i, and the normalization r^{-d} in the definition of $c(z, y; r)$. Conditional on X_t and the set of patch locations $\{z_i\}_{i=1}^n$, the $X_{i,t+1}$ $(i = 1, \ldots, n)$ are independent with transition probabilities

$$\mathbb{P}\left(X_{i,t+1} = 1 \mid X_t, z_1, \ldots, z_n\right) \;=\; f(S_i(X_t))\,(1 - X_{i,t}) + (1 - e(z_i))X_{i,t}. \tag{2.2}$$

If patch i is occupied at time t, then that population survives to time $t+1$ with probability $1 - e(z_i)$. Otherwise, it is colonised with probability $f(S_i(X_t))$.

Alonso and McKane [1, section 6.3] proposed a continuous time analogue of the incidence function model. Their model is a continuous time Markov chain $X(t) = (X_1(t), \ldots, X_n(t))$

on $\mathcal{X}$, whose transition rates in the above setting are given by

$$\begin{aligned} X &\to X + \delta_i^n \qquad \text{at rate} \qquad f(S_i(X))(1 - X_i); \\ X &\to X - \delta_i^n \qquad \text{at rate} \qquad e(z_i)X_i, \end{aligned} \tag{2.3}$$

and δ_i^n is the vector of length n with 1 at position i and zeros elsewhere.

Since both processes are finite state Markov processes, with the extinction state absorbing and accessible from all other states, the extinction state is almost surely eventually reached. However, in many circumstances, the processes may remain for long periods in an apparent stochastic equilibrium, a quasi-stationary distribution. In [2], it is shown that the stochastic processes can be well approximated by corresponding deterministic systems, at least over bounded time intervals. Thus, if the stochastic processes have initial conditions corresponding to any equilibrium of the deterministic systems, they remain close to this equilibrium over bounded time intervals, with asymptotically high probability. In this paper, working under conditions which guarantee at most one equilibrium of the deterministic systems other than extinction, we address the problem of describing the equilibrium.

The deterministic approximation of the Markov chain defined by (2.2) was proposed by Ovaskainen and Hanski [14]. Let $p_{i,t}$ be the probability that patch i is occupied at time t and let $p_t = (p_{1,t}, \ldots, p_{n,t})$. As in the incidence function model, they model the change in p_t by

$$p_{i,t+1} - p_{i,t} \;=\; f(S_i(p_t))(1 - p_{i,t}) - e(z_i)p_{i,t}. \tag{2.4}$$

For the continuous time metapopulation model (2.4), the deterministic approximation is provided by the spatially realistic Levins model [7]. This model is a system of ordinary differential equations

$$\frac{dp_i(t)}{dt} \;=\; f(S_i(p(t)))(1 - p_i(t)) - e(z_i)p_i(t), \tag{2.5}$$

for $p\colon \mathbb{R}_+ \to [0,1]^n$. The equilibrium levels of both these deterministic models are given by the fixed points p_n^* of the function $E_n : [0,1]^n \to [0,1]^n$, where

$$E_n(p)_i \;:=\; \frac{f\Big((A/(n-1))\sum_{j\neq i} a(z_j)c(z_i, z_j; r)p_j\Big)}{e(z_i) + f\Big((A/(n-1))\sum_{j\neq i} a(z_j)c(z_i, z_j; r)p_j\Big)}.$$

Define the matrix $T_{ij} = f'(0)(A/(n-1))a(z_j)c(z_i; z_j; r)/e(z_i)$ for $i \neq j$ and $T_{ii} = 0$, and let $\lambda(T)$ be the Frobenius-Perron eigenvalue of T. When f is continuous and concave and

T is primitive, that is if T^k is a positive matrix for some k, the cone limit set trichotomy [8, Theorem 6.3] can be applied to conclude that

- If $\lambda(T) \leq 1$, then $0 \in \mathbb{R}^n$ is the only fixed point of E_n;
- If $\lambda(T) > 1$, then, in addition to 0, E_n has a non-zero fixed point.

In what follows, we denote the largest fixed point of E_n by p_n^*. Our aim is to determine good approximations to p_n^*. We do so under certain assumptions.

(A) Independent patch locations: The patch locations z_i are independently distributed over the *connected* set Ω, with probability density $A^{-1}\sigma(\cdot)$.

We then define

$$\rho(z) \;:=\; \int_\Omega a(y)c(z,y;r)\sigma(y)\,dy. \tag{2.6}$$

(B) Bounded support of colonisation kernel: For all $z \in \Omega$, $c_z(x) > 0$ for all $x \in [0,1)$ and $c_z(x) = 0$ for all $x > 1$.

(C) Smoothness: The functions e, a, f, σ and ρ are continuously differentiable on Ω. Their respective Lipschitz constants are denoted by L_e, L_a, L_f, L_σ and L_ρ. The colonisation kernel $c_z(x)$ is uniformly continuous on $\Omega \times [0,1)$.

(D) Bounded: The functions e, σ and a are bounded above by $e_{\max}, \sigma_{\max}$ and $a_{\max}$ and below by *positive* constants $e_{\min}, \sigma_{\min}$ and $a_{\min}$, respectively. The function c_z is bounded above by $c_{\max}$, for each $z \in \Omega$.

(E) Concave colonisation function: f is an increasing concave function such that $f(0) = 0$, and $f(0) > 0$ for all $x > 0$.

Note that, from Assumption E, there is a constant $C_1 > 0$ such that $f(x) \geq f'(0)x - C_1x^2$ for all $x \geq 0$, and that $L_f = f'(0)$.

The quantities in the set $\mathcal{Q} := \{L_f, \sigma_{\max}, a_{\max}, e_{\max}, \sigma_{\min}, a_{\min}, e_{\min}, c_{\max}\}$ can all be taken to be fixed without reference to the values of n, r and A. However, the Lipschitz constants L_e, L_a, L_σ and L_ρ measure the maximum possible changes in the corresponding functions per unit displacement of the arguments, and have units $\{\text{distance}\}^{-1}$. Correspondingly, we shall take rL_e, rL_a, rL_σ and rL_ρ rather than L_e, L_a, L_σ and L_ρ to be the quantities of biological interest. The error in our approximations is measured in terms of these quantities; in particular, certain inequalities between them must be satisfied, if our approximation bounds are to be valid. However, we shall tacitly think of n and the combination nr^d/A being big, and of $r^d/A, rL_e, rL_a, rL_\sigma$ and rL_ρ being small, all of which are needed if our approximation errors are to be small. In essence, we establish conditions under which the probability of a patch at location z being occupied is the same as would be the case if the environment were locally constant, with the values taken at z, and if the patches were not discrete, but were smeared over the habitat according to the density function σ. Thus we want rL_e, rL_a, rL_σ and rL_ρ to be small (within the colonization radius, environmental conditions do not vary a lot), and nr^d/A to be big (many patches averaging to realize the colonization pressure). The requirement that r^d/A be small is needed to prevent boundary effects dominating the final result.

3. Approximation of the equilibrium

To construct our approximation, we first define the function $F(\cdot;\tau,\nu)\colon\ [0,\infty) \to [0,1]$ by

$$F(x;\tau,\nu) \ := \ \frac{f(\tau x)}{\nu + f(\tau x)}.$$

This function has a fixed point at 0 and, if $f'(0)\tau > \nu$, then it also has a non-zero fixed point. We now define the function $q_\alpha\colon\ \Omega \to [0,1]$ such that $q_\alpha(z)$ is the largest fixed point of $F(\cdot;\rho(z),\alpha e(z))$, for fixed $\alpha > 0$. We would ideally like to show that $q_1(z_i)$ is a good approximation to p_i. To do so, we establish upper and lower bounds, one using $q_\alpha(z_i)$, with α less than, but close to, 1, and the other using $q_\beta(z_i)$, for β close to, but larger than, 1. More precisely, we first show that, with high probability, the function $p^+_{\alpha_1,\alpha_2}\colon\ \Omega \to [0,1]$, defined as

$$p^+_{\alpha_1,\alpha_2}(z) \ := \ q_{\alpha_1}(z) \vee (1-\alpha_2),$$

provides an upper bound on p^*_n for some α_1 and α_2 such that $1/2 < \alpha_2 \le \alpha_1 < 1$; that is, that $p^*_{i,n} \le p^+_{\alpha_1,\alpha_2}(z_i)$ for all i. To construct a lower bound on p^*_n, we then choose some $\Theta \subset \Omega$ with a smooth boundary $\partial\Theta$. For $m > 0$ and $\beta > 1$, we define the function $p^-_{\Theta,\beta,m}\colon\ \Theta \to [0,1]$ by

$$p^-_{\Theta,\beta,m}(z) \ := \ (m\|z - \partial\Theta\| \wedge q_\beta(z)),$$

where $\|z - \partial\Theta\|$ is the distance from z to the boundary of Θ. The aim is then to find choices of β and m such that $p^-_{\Theta,\beta,m}$ provides a lower bound on p^*_n with high probability.

Theorem 3.1 (Upper bound). *Let $N(\Omega, r)$ is the number of balls of radius r required to cover Ω. Suppose that Assumptions A–E hold and that $n > 2N(\Omega, r/3)$. Define*

$$\eta_\Omega \;:=\; \min_{z\in\Omega} q_1(z); \quad \rho_{\max} \;:=\; a_{\max} c_{\max} \sigma_{\max} v_d, \tag{3.1}$$

where v_d is the volume of the d-dimensional unit ball. Assume that

$$2L_f L_q r \rho_{\max} \;\le\; e_{\min}(1-\alpha_1)(\alpha_1 \eta_\Omega \vee (1-\alpha_2)); \tag{3.2}$$

where

$$L_q \;:=\; \frac{\sqrt{d}}{e_{\min}} \left(2L_f L_\rho + L_e\right). \tag{3.3}$$

Then, if $L_f \rho_{\max}/e_{\min} > 1/2$,

$$\mathbb{P}\big(p^*_{n,i} \le p^+_{\alpha_1,\alpha_2}(z_i) \text{ for all } i = 1,\dots,n\big) \;\ge\; 1 - 2n\exp\left(-C_2 \frac{(n-1)r^d}{A}\, \frac{e^2_{\min}(1-\alpha_1)^2}{16 a^2_{\max} L_f^2}\right)$$
$$- \frac{n}{2} \exp\left(-n \inf_{z\in\Omega} A^{-1} \int_\Omega \mathbb{I}(\|y-z\| \le r/3)\sigma(y)\, dy\right),$$

where

$$C_2 \;:=\; \{3\{c_{\max}\}^2 \sigma_{\max} v_d\}^{-1}.$$

If $L_f \rho_{\max}/e_{\min} \le 1/2$, then

$$\mathbb{P}\left(p^*_{n,i} = 0 \text{ for all } i = 1,\dots,n\right) \ge\; 1 - 2n\exp\left\{-C_2 \frac{(n-1)r^d}{A} \left(\frac{\rho_{\max}}{2a_{\max}}\right)^2\right\}$$
$$- \frac{n}{2} \exp\left(-n \inf_{z\in\Omega} A^{-1} \int_\Omega \mathbb{I}(\|y-z\| \le r/3)\sigma(y)\, dy\right).$$

If $\eta_\Omega > 0$, inequality (3.2) in Theorem 3.1 can be satisfied with $\alpha_2 = \alpha_1$, by taking $1-\alpha_1$ to be as big as a multiple of $L_q r$. If $\eta_\Omega = 0$, then we must take $(1-\alpha_1)(1-\alpha_2)$ to be bigger than a multiple of $L_q r$. However, as $1-\alpha_1$ increases, so does the difference between $q_1(z)$ and $q_{\alpha_1}(z)$, and the upper bound becomes correspondingly less tight. For $p^+_{\alpha_1,\alpha_2}$ to be an upper bound with high probability, we need $(1-\alpha_1)^2(nr^d/A)$ to be large. For sufficiently regular regions Ω, $N(\Omega, r/3) \le cAr^{-d}$ for some constant $c > 0$, and so the assumption that $n > 2N(\Omega, r/3)$ would normally be satisfied in situations where we expect the bound to hold with high probability.

Finally, defining $B_x(t) := \{z : \|z - x\| \le t\}$, we note that if Ω is r-smooth, in the sense that, for some $\Omega' \subset \Omega$,

$$\Omega = \bigcup_{x\in\Omega'} B_x(t_x), \qquad \text{with} \quad t_x \ge r \text{ for all } x \in \Omega',$$

then

$$\int_\Omega \mathbb{I}(\|y - z\| \le r/3)\, dy \;\ge\; c_d r^d \quad \text{for all } z \in \Omega,$$

where c_d is a geometric constant depending only on d. In such circumstances,

$$n \inf_{z\in\Omega} A^{-1} \int_\Omega \mathbb{I}(\|y - z\| \le r/3)\sigma(y)\, dy \;\ge\; c_d\sigma_{\min}(nr^d/A). \tag{3.4}$$

The lower bound is more complicated to state, because boundary effects make themselves felt. We restrict ourselves to proving lower bounds for $p^*_{i,n}$ for points z_i belonging to sets of the form $\Theta := \Theta_{x,t} := B_x(t)$, where $x \in \Omega$ and $t > 0$ are such that $\Theta \subseteq \Omega$. For different choices of $\Theta_{x,t} \ni z_i$, the lower bounds may be different, in which case the largest can be taken. Broadly speaking, if the set $\Theta_{x,t}$ is such that the metapopulation is sufficiently locally viable throughout it, in that

$$\eta_{\Theta_{x,t}} := \inf_{z\in\Theta_{x,t}} q_1(z)$$

is not close to zero, and if z_i is not too close to its boundary $\partial\Theta_{x,t}$, then the lower bound is reasonably close to $q_1(z_i)$.

Suppose that we have such a Θ. Then, for each $1 \le \beta \le 1 + \frac{1}{2}\eta_\Theta$, we can define a positive quantity $\epsilon_{\Theta,\beta}$ in terms of the parameters of the process, that is at least as big as a positive multiple of η^2_Θ, provided that $r/t, L_q r, L_\sigma r$ and $L_a r$ are all small enough; the detailed requirements are in the statement of Lemma 7.3 given in Section 7. With this $\epsilon_{\Theta,\beta}$, we have the following result.

Theorem 3.2. *Suppose that* $\inf_{z\in\Theta} q_1(z) =: \eta_\Theta > 0$, *that* $1 < \beta < \beta' < 1 + \eta_\Theta/2$, *and that* $L_f\rho_{\max}/e_{\min} > 1/2$. *Assume that inequalities (7.22)–(7.24), (7.28) and (7.29) hold. Then, with*

$$m := \frac{e^2_{\min}\eta_\Theta(\beta' - \beta)}{4r\rho^2_{\max}L_f(C_1\rho_{\max} + L_f)},$$

we have

$$\mathbb{P}\left(p^*_{i,n} \ge p^-_{\Theta,\beta',m}(z_i) \text{ for all } z_i \in \Theta\right) \;\ge\; 1 - 2n\exp\left(-C_2\frac{(n-1)r^d}{A}\,\frac{C_4^2 e^2_{\min}\eta^4_\Theta(\beta-1)^2}{a^2_{\max}L_f^2}\right),$$

where C_2 *is as in Theorem 3.1 and* C_4 *is a function of the elements of* $\mathcal{Q}$, *given in (7.25).*

Theorems 3.1 and 3.2 can be combined in the following corollary.

Corollary 3.3. *Suppose that the conditions of Theorems 3.1 and 3.2 hold, with* $\alpha_2 = 1-\eta_\Theta < \alpha_1 < 1$ *and with* β, β' *and* m *as above. Define* $\Theta_m := \{z \in \Theta : \|z - \partial\Theta\| \geq m^{-1}\}$, *where* $\Theta = B_x(t)$ *and* $t > r + m^{-1}$. *Then*

$$\begin{aligned} &\mathbb{P}\left(\left|p^*_{i,n} - q_1(z_i)\right| \leq \alpha_1^{-1}(\beta' - \alpha_1) \text{ for all } z_i \in \Theta_m\right) \\ &\quad \geq\ 1 - 4n \exp\left(-\frac{C_2(n-1)r^d e^2_{\min}}{Aa^2_{\max}L_f^2}\left(C_4^2\eta_\Theta^4(\beta-1)^2 \wedge \frac{(1-\alpha_1)^2}{16}\right)\right) \\ &\qquad - \frac{n}{2}\exp\left(-c_d\sigma_{\min}(nr^d/A)\right). \end{aligned}$$

The inequalities (7.22)–(7.24), (7.28) and (7.29) require that there are constants C_q and C_{rt}, functions only of the parameters in the set $\mathcal{Q}$, such that

$$L_\rho r + L_e r \ \leq\ C_q\eta_\Theta(\eta_\Theta \wedge (\beta' - \beta)); \quad r/t \ \leq\ C_{rt}(\eta_\Theta \wedge (\beta' - \beta)). \tag{3.5}$$

As Corollary 3.3 shows, the approximation accuracy is better the closer β' and α_1 are to 1, whereas the probability that this accuracy is realized is reduced and the restrictions on $L_\rho r + L_e r$ becomes more stringent as β' and α_1 become closer to 1. Furthermore, if β' becomes closer to 1, the subset of Ω over which the approximation applies is smaller and the restriction on r/t becomes more stringent.

To illustrate the implications of these general results, we give a further consequence, expressed in the form of a limit theorem. We think of a sequence of processes, indexed by n, in which the parameters in $\mathcal{Q}$ are held constant, as are L_ρ and L_e, while the density of patches n/A_n increases. Under such circumstances, it is reasonable to suppose that the colonization radius r_n decreases, since migrants can find other patches closer to home, but in such a way that $M_n := nr_n^d/A_n$ increases.

The set Ω_n is assumed to be somewhat more than r_n-smooth, in that we suppose that

$$\Omega_n \ =\ \bigcup_{i=1}^{X_n} B_{x(i,n)}(t(i,n)),$$

with $X_n < \infty$ and $t(i,n) \geq t_n$ for each i, where $r_n/t_n \leq 1$ decreases with n. The overlap in the union is also assumed not to be too great, in the sense that

$$\sum_{i=1}^{X_n} v_d\{t(i,n)\}^d \ \leq\ kA_n,$$

for some k not depending on n. In consequence, for some k' not depending on n,

$$N(\Omega, r_n/3) \;\le\; k'A_n/r_n^d \;=\; k'n/M_n \;=\; O(n) \quad \text{as } n \to \infty.$$

Corollary 3.4. *Under the above circumstances, suppose that $r_n \to 0$ as $n \to \infty$ and that t_n is bounded away from 0. Assume also that, for all n, $\eta_{\Omega_n} \ge c_1 r_n^{\gamma_1}$ for some $\gamma_1 \in [0, 1/2)$ and $c_1 > 0$, and that*

$$r_n^{2(1+\gamma_1)} \phi_n^2 M_n \;\ge\; c_2(\log n)^{1+\gamma_2}, \tag{3.6}$$

for some $c_2, \gamma_2 > 0$. Then there exist constants $K_1, K_2 < \infty$ such that, for any sequence $\phi_n \to \infty$ such that $r_n^{1-2\gamma_1}\phi_n \to 0$,

$$\mathbb{P}\left(\left|p^*_{i,n} - q_1(z_{i,n})\right| \le K_1 r_n^{1-\gamma_1}\phi_n \text{ for all } z_i \in \Omega'_n\right) \;\to\; 1,$$

where

$$\Omega'_n \;:=\; \{z \in \Omega\colon\, \|z - \partial\Theta^{(i,n)}\| \ge K_2/\phi_n \text{ for some } 1 \le i \le X_n\}.$$

Thus, under such conditions, the error in the approximation converges to zero with $r_n^{1-\gamma_1}\phi_n$, and the proportion of Ω_n for which the approximation does not hold converges to zero with $1/\phi_n$ — faster, if $t_n \to \infty$. When $\eta_{\Omega_n} \to 0$ as $n \to \infty$, the uniform precision is reduced. However, Corollary 3.4 could still be applied to any sequence of subsets $\widetilde{\Omega}_n \subset \Omega_n$ for which $\eta_{\widetilde{\Omega}_n}$ remains bounded away from zero, showing that the error is typically smaller where $q_1(z)$ is larger. Indeed, this illustrates the flexibility of our theorems.

Analogous results can also be proved in the limit in which the landscape becomes smoother, much as in Ovaskainen and Cornell [12], without necessarily requiring that $r_n \to 0$. Assume instead that

$$s_n \;:=\; \max\{r_n/t_n,\, (L_\rho^{(n)} + L_e^{(n)})r_n\} \;\to\; 0 \quad \text{as } n \to \infty.$$

Then the statement of Corollary 3.4 holds, with s_n in place of r_n.

4. Discussion

Both upper and lower bounds require the functions e and ρ to be smooth. One biologically relevant situation in which this need not be the case would be for terrestrial animals on islands, where, at the boundaries between sea and land, the patch density σ can be expected to change abruptly from a positive value to 0. This is not a problem for the lower bound, since the argument can be carried out within any subset of the region Ω

on which the functions ρ and e are smooth. For the upper bound, the argument given can be applied to any island Ω' over which the functions ρ and e are smooth, if $\sigma(z) = 0$ at all points outside Ω' to a distance of at least r; the proof of Theorem 3.1 indeed assumes that there is no contribution to the metapopulation coming from outside Ω. On the intervening parts of Ω, in which the patch density σ is zero, there are no patches whose probability of occupancy is to be bounded. If there are boundaries across which the values of the functions ρ and e change abruptly, but not because σ jumps to zero, the upper bound argument would have to be modified in much the same spirit as that for the lower bound, but we have not attempted to do this.

Even when the region containing the habitat patches is connected, parts of the metapopulation can be rendered effectively disconnected by regions of low patch density, low colonisation rates and high extinction rates. In such circumstances, the deterministic metapopulation model may still possess a unique non-zero equilibrium. However, if the associated stochastic metapopulation model is initially in a state in which only some of the viable regions are occupied, the remaining viable regions are likely to remain uncolonized for a very long time, so that the stochastic metapopulation model has quasi-equilibria that are not well approximated by the equilibria of the deterministic system.

Our bounds on the equilibrium can be used to deduce bounds on the rate at which the metapopulation returns to equilibrium after a small displacement. Ovaskainen and Hanski [15] refer to this as the 'characteristic response time'. Near equilibrium, the continuous time system (2.5) can be appoximately expressed as

$$\frac{d(p_i(t) - p_i^*)}{dt} \;\approx\; \mathcal{J}(p^*)(p(t) - p^*),$$

where

$$\mathcal{J}(p) \;=\; \begin{cases} -\left(f(S_i(p^*)) + e(z_i)\right), & i = j \\ f'(S_i(p^*))(1 - p_i^*)\frac{A}{(n-1)}a(z_j)c(z_i, z_j; r), & i \neq j. \end{cases}$$

Now suppose that we have functions p^- and p^+ such that $p^-(z_i) \le p_i^* \le p^+(z_i)$ for all $1 \le i \le n$. Since, under Assumption E, f is increasing and concave, $\mathcal{J}(p^+) \le \mathcal{J}(p^*) \le \mathcal{J}(p^-)$, where the inequality is interpreted elementwise. Now, for any C_5 chosen larger than $\max_{1 \le i \le n}\{f(S_i(p^+)) + e(z_i)\}$, the matrix $C_5 I + \mathcal{J}(p^+)$ is non-negative and primitive. By Seneta [16, Theorem 1.1(e) of Chapter 1] it follows that $\lambda(\mathcal{J}(p^+)) \le \lambda(\mathcal{J}(p^*)) \le \lambda(\mathcal{J}(p^-))$, where $\lambda(\cdot)$ denotes the leading eigenvalue. Thus we are able to bound the 'characteristic response time' $1/\lambda(\mathcal{J}(p^*))$ of Ovaskainen and Hanski [15], using p^- and p^+. A similar argument can be made for the discrete time system (2.4), provided that $f(S_i(p^+)) + e(z_i) \leq 1$ for all i; this ensures that the Jacobian is a non-negative matrix.

If the function f is linear and $e(z) = \nu$ is constant in z, $q_1(z)$ as defined in Section 3 is a concave function of $\rho(z)$, provided that $\rho(z) > \nu/L_f$. Jensen's inequality then implies that the equilibrium probability of patch occupancy, averaged over a region in which $\rho(z)$ is uniformly above ν/L_f, is smaller than the equilibrium probability of patch occupancy in a landscape with a constant colonisation rate equal to the spatial average. In this sense, spatial variability reduces the occupation level of the metapopulation when f is linear. However, for strictly concave f satisfying Assumption E, $q_1(z)$ is not necessarily concave whenever $\rho(z) > \nu/L_f$.

In the model that we discuss, randomness appears only through the positions of the patches in the smooth landscape. However, it would also be interesting to allow for the possibility that, although the landscape is smooth 'on average', individual patches may have properties that differ from the average; for instance, the local extinction rates could be modelled as being random, with a mean that varies smoothly within the region. It would also be interesting to allow the patch locations to be chosen as a sample from a point process with more dependence structure.

Another way in which additional randomness could be incorporated into the landscape is by allowing the landscape to change over time, as in [4]. A common model for landscape dynamics is to allow habitat patches to change between 'suitable' and 'unsuitable' states, following a Markov chain (for example, [10]). When a habitat patch becomes 'unsuitable', any local population occupying that habitat patch becomes extinct, and the patch cannot be recolonised until it becomes 'suitable' again. Xu et al. [17] incorporated this type of dynamics into the spatially realistic Levins model. Letting $h(t, z_i)$ denote the probabilty that the habitat patch at z_i is 'suitable', their system of equations becomes

$$\frac{dp_i(t)}{dt} = f(S_i(p(t)))(h(t, z_i) - p_i(t)) - \tilde{e}(z_i)p_i(t),$$

where $\tilde{e}(z_i)$ incorporates the rate of destruction of habitat patch i, in addition to the rate of local extinction $e(z_i)$ at patch i. Since $h(t, z)$ converges to some $h(z)$ as $t \to \infty$, the equilibrium probabilities for the spatially realistic Levins model with landscape dynamics are a fixed point of the function $\widetilde{E}_n$ given by

$$\widetilde{E}_n(p)_i \;:=\; \frac{h(z_i)f\Big((A/(n-1))\sum_{j\neq i}a(z_j)c(z_i,z_j;r)p_j\Big)}{\tilde{e}(z_i)+h(z_i)f\Big((A/(n-1))\sum_{j\neq i}a(z_j)c(z_i,z_j;r)p_j\Big)}.$$

It would thus be relatively straightforward to extend our analysis to bound the equilibria of the deterministic model in Xu et al. [17]. In particular, if f is linear, then the equilibrium is approximated by $1-\tilde{e}(z_i)/(h(z_i)\rho(z_i))$.

5. Appendix: Auxiliary results

Lemma 5.1. *Suppose that Assumption E holds. Let q denote the largest fixed point of $F(\cdot;\tau,\nu)$. Then $q \le x$ if $(1-x)f(\tau x) \le \nu x$ and $q \ge x$ if $(1-x)f(\tau x) \ge \nu x$.*

Proof. Since f is concave, increasing and not identically zero, by Assumption E, $F(\cdot;\tau,\nu)$ is concave, and strictly concave at 0. Hence $g(x) := F(x;\tau,\nu) - x$ is concave, strictly concave at zero, and has $g(0)=0$ and $g(\infty)=-\infty$. If $g'(0)=F'(0;\tau,\nu)-1\le 0$, there is thus no other solution to $g(x)=0$. If $g'(0)>0$, there is exactly one other solution q, and $g(x)>0$ for $0<x<q$, and $g(x)<0$ for $x>q$. Thus, $0<x<q$ if and only if $g(x)>0$, and so

$$F(x;\tau,\nu) \;=\; \frac{f(\tau x)}{\nu+f(\tau x)} \;>\; x,$$

implying that $(1-x)f(\tau x) > \nu x$; similarly, $q<x$ if and only if $g(x)<0$ and $(1-x)f(\tau x) < \nu x$.

□

Lemma 5.2. *Suppose that Assumptions C, D and E hold. Then, for all $\alpha \ge 1/2$, q_α is Lipschitz continuous on $\{z\in\Omega : q_\alpha(z)>0\}$, with Lipschitz constant at most L_q, as defined in (3.3).*

Proof. We write $F_\alpha(q,z) := F(q;\rho(z),\alpha e(z))$, where $F_\alpha\colon [0,1]\times\mathbb{R}^d \to \mathbb{R}_+$. For functions $g\colon [0,1]\times\mathbb{R}^d\to\mathbb{R}_+$, we denote by $D_q g$ the partial derivative of g with respect to its first argument, and by $D_j g$ the partial derivative in the direction of the j-th coordinate axis in $\mathbb{R}^d$, $1\le j\le d$. By the implicit function theorem, $q_\alpha(z)$ is continuously differentiable in an open neighbourhood of z, with

$$(D_j q_\alpha)(z) \;=\; -\left[(D_qF_\alpha)(q_\alpha(z),z)-1\right]^{-1}(D_jF_\alpha)(q_\alpha(z),z), \quad 1\le j\le d, \tag{5.1}$$

provided that

$$(D_q F_\alpha)(q_\alpha(z), z) \neq 1. \tag{5.2}$$

For any $z \in \Omega$ and $q \in [0,1]$,

$$(D_q F_\alpha)(q, z) = \frac{\alpha e(z)\rho(z) f'(q\rho(z))}{(\alpha e(z) + f(q\rho(z)))^2}.$$

As $q_\alpha(z) = F(q_\alpha(z); \alpha e(z), \rho(z))$,

$$\begin{aligned}(D_q F_\alpha)(q_\alpha(z), z) &= \frac{(1 - q_\alpha(z))\rho(z) f'(q_\alpha(z)\rho(z))}{(\alpha e(z) + f(q_\alpha(z)\rho(z)))} \\ &= \frac{(1 - q_\alpha(z)) q_\alpha(z)\rho(z) f'(q_\alpha(z)\rho(z))}{f(q_\alpha(z)\rho(z))}.\end{aligned}$$

By the mean value theorem, there exists a $\tilde{q} \in (0, q_\alpha(z))$ such that

$$f'(\tilde{q}\rho(z)) = \frac{f(q_\alpha(z)\rho(z))}{q_\alpha(z)\rho(z)}.$$

As f is concave, $f'(\tilde{q}\rho(z)) \geq f'(q_\alpha(z)\rho(z))$. Therefore,

$$(D_q F_\alpha)(q_\alpha(z), z) \leq 1 - q_\alpha(z), \tag{5.3}$$

and (5.2) holds for any $z \in \Omega$ such that $q_\alpha(z) > 0$. Differentiating F_α in direction j yields

$$(D_j F_\alpha)(q, z) = \frac{\alpha e(z) q (D_j\rho)(z) f'(q\rho(z)) - \alpha (D_j e)(z) f(q\rho(z))}{(\alpha e(z) + f(q\rho(z)))^2}.$$

Evaluating this derivative at $(q_\alpha(z), z)$ gives

$$\begin{aligned}(D_j F_\alpha)(q_\alpha(z), z) &= \frac{\alpha e(z) q_\alpha(z) (D_j\rho)(z) f'(q_\alpha(z)\rho(z)) - \alpha (D_j e)(z) f(q_\alpha(z)\rho(z))}{(\alpha e(z) + f(q_\alpha(z)\rho(z)))^2} \\ &= q_\alpha(z) \frac{(1 - q_\alpha(z))(D_j\rho)(z) f'(q_\alpha(z)\rho(z)) - \alpha (D_j e)(z)}{(\alpha e(z) + f(q_\alpha(z)\rho(z)))}. \end{aligned} \tag{5.4}$$

Combining equations (5.1) and (5.4) with the bound (5.3) yields

$$|(D_j q_\alpha)(z)| \leq \frac{1}{e(z)} \left(\frac{L_f}{\alpha} |(D_j\rho)(z)| + |(D_j e)(z)| \right) \leq \frac{1}{e_{\min}} (\alpha^{-1} L_f L_\rho + L_e).$$

Therefore, for any $\alpha \geq 1/2$, q_α is Lipschitz on $\{z \in \Omega : q_\alpha > 0\}$ with the Lipschitz constant given in (3.3). $\square$

Lemma 5.3. *Suppose that Assumption E holds and that $q_1(z) \geq \eta > 0$. Then, for any $\beta \in (1, (1-\eta)^{-1})$, $q_\beta(z) \geq \beta\eta + 1 - \beta$, and, for any $\alpha \in (0,1)$, $q_\alpha(z) \geq \alpha\eta$.*

Proof. For any $\beta \in (1, (1-\eta)^{-1})$, it follows that $0 < \beta\eta + 1 - \beta < \eta$ and that, by Assumption E,

$$f\left(\rho(z)(\beta\eta + 1 - \beta)\right) \;\geq\; \left(\beta + \frac{1-\beta}{\eta}\right) f(\rho(z)\eta).$$

As $q_1(z) \geq \eta$, we can apply Lemma 5.1 to give $f(\rho(z)\eta) \geq e(z)\eta/(1-\eta)$, and hence

$$\begin{aligned} f\left(\rho(z)(\beta\eta + 1 - \beta)\right) &\;\geq\; \left(\beta + \frac{1-\beta}{\eta}\right) \frac{e(z)\eta}{1-\eta} \\ &\;=\; (\beta\eta + 1 - \beta)\frac{e(z)}{1-\eta} \;=\; \frac{\beta e(z)(\beta\eta + 1 - \beta)}{1 - (\beta\eta + 1 - \beta)}. \end{aligned}$$

Applying Lemma 5.1 again, we see that $q_\beta(z) \geq \beta\eta + 1 - \beta$.

For $\alpha \in (0,1)$ we follow similar reasoning to show that

$$f(\rho(z)\alpha\eta) \;\geq\; \alpha f(\rho(z)\eta) \;\geq\; \alpha e(z)\eta/(1-\eta) \;\geq\; \alpha e(z)\alpha\eta/(1-\alpha\eta),$$

and applying Lemma 5.1 we see that $q_\alpha(z) \geq \alpha\eta$. $\square$

In the following we let $\sigma_{n\backslash i} := \frac{A}{(n-1)} \sum_{j \neq i} \delta_{z_j}$, which is A times the empirical measure of patches excluding patch i.

Lemma 5.4. *Suppose that Assumptions A, B and D hold. Then, for any* $h\colon \Omega \to [0, H]$, $0 < t \leq H c_{\max} \sigma_{\max} v_d$ *and* $z \in \Omega$,

$$\mathbb{P}\left(\left|\int c(z, y; r) h(y)[\sigma_{n\backslash i}(dy) - \sigma(y)\,dy]\right| \;\geq\; t\right) \leq 2\exp\left(-C_2((n-1)r^d/A)(t/H)^2\right),$$

where

$$C_2 \;:=\; \{3\{c_{\max}\}^2 \sigma_{\max} v_d\}^{-1}.$$

Proof. Note first that, for patches distributed independently with density $A^{-1}\sigma(\cdot)$, we have

$$\mathbb{E}\left\{\int c(z, y; r) h(y) \sigma_{n\backslash i}(dy)\right\} \;=\; \int c(z, y; r) h(y) \sigma(y)\,dy.$$

The left hand side of this expression is a sum of i.i.d. random variables, each bounded by $H c_{\max} A/((n-1)r^d)$, and each with variance at most $\{H c_{\max} A/((n-1)r^d)\}^2 \sigma_{\max} v_d r^d / A$, where, as before, v_d denotes the volume of the unit ball in $\mathbb{R}^d$. Hence, applying McDiarmid

[11, Theorem 2.7], it follows that, for any $t > 0$,

$$\begin{aligned}
&\mathbb{P}\left(\left|\int c(z,y;r)h(y)\sigma_{n\setminus i}(dy) - \int c(z,y;r)h(y)\sigma(y)\,dy\right| > t\right)\\
&\quad\leq\; 2\exp\left(-\frac{t^2}{2((n-1)\{Hc_{\max}A/((n-1)r^d)\}^2\sigma_{\max}v_d A^{-1}r^d + \{Hc_{\max}A/((n-1)r^d)\}t/3)}\right)\\
&\quad\leq\; 2\exp\left(-\frac{t^2}{3(A/(n-1)r^d)\{Hc_{\max}\}^2\sigma_{\max}v_d}\right)\\
&\quad=\; 2\exp\left(-C_2((n-1)r^d/A)(t/H)^2\right)
\end{aligned}$$

if $t/H \leq c_{\max}\sigma_{\max}v_d$. □

Lemma 5.5. *Suppose Assumptions A, B and D hold. Let $N(\Omega, r)$ be the number of balls of radius r required to cover Ω. If $n > 2N(\Omega, r/3)$, then T is primitive with probability at least*

$$1 - N(\Omega, r/3)\exp\left(-n\inf_{z\in\Omega} A^{-1}\int_{\Omega}\mathbb{I}(\|y-z\| \leq r/3)\sigma(y)dy\right) \tag{5.5}$$

Proof. Let $\tilde{T}$ be the incidence matrix of T, that is $\tilde{T}_{ij} = 1$ if $T_{ij} > 0$ and $T_{ij} = 0$ otherwise. The matrix T is primitive if $\tilde{T}$ is both irreducible and acyclic [16, Theorem 1.4 of Chapter 1]. By Assumptions B and D, $\tilde{T}$ is symmetric and $\tilde{T}_{ii} = 0$. Define the graph $\mathcal{G} = (V, E)$ where $V := \{z_1, \ldots, z_n\}$ and $(z_i, z_j) \in E$ if and only if $\|z_i - z_j\| \leq r$. The matrix $\tilde{T}$ is the adjacency matrix of $\mathcal{G}$ and is irreducible if $\mathcal{G}$ is connected. Let $N := N(\Omega, r/3)$ and $y_1, \ldots, y_N \in \Omega$ such that $\Omega \subset \cup_i^N B(y_i, r/3)$, where $B(y, r)$ is a closed ball of radius r centered at y. Define the graph $\hat{\mathcal{G}} = (\hat{V}, \hat{E})$ where $\hat{V} = \{y_1, \ldots, y_N\}$ and $(y_i, y_j) \in \hat{E}$ if and only if $\|y_i - y_j\| \leq r/3$. Since Ω is connected, the graph $\hat{\mathcal{G}}$ is also connected. Suppose that each ball $B(y_i, r/3)$ contains at least one element of V. For any z_i and z_j, there exists a path $\{y_{k_0}, y_{k_1}, \ldots, y_{k_{m+1}}\}$ in $\hat{\mathcal{G}}$ such that $z_i \in B(y_{k_0}, r/3)$ and $z_j \in B(y_{k_{m+1}}, r/3)$. Taking any $z_{k_\ell} \in B(y_{k_\ell}, r/3)$, we have constructed a path $\{z_i, z_{k_1}, \ldots, z_{k_m}, z_j\}$ in $\mathcal{G}$, since

$$\|z_{k_\ell} - z_{k_{\ell+1}}\| \leq \|z_{k_\ell} - y_{k_\ell}\| + \|y_{k_\ell} - y_{k_{\ell+1}}\| + \|y_{k_{\ell+1}} - z_{k_{\ell+1}}\| \leq r.$$

Thus $\mathcal{G}$ is connected and $\tilde{T}$ is irreducible if each ball $B(y_i, r/3)$ contains at least one element of V. This occurs with probability at least that given in (5.5).

To show that $\tilde{T}$ is acyclic, it is sufficient to show that $\tilde{T}^2_{ii} > 0$ and $\tilde{T}^3_{ii} > 0$ for some i, since $\tilde{T}$ is irreducible [16, Lemma 1.2 of Chapter 1]. This is true if there are three elements of V that are within distance r of each other. Since $n > 2N(\Omega, r/3)$, there is at least one $B(y_i, r/3)$ which contains at least three elements of V, and these are within distance $2r/3$ of each other, completing the proof. □

6. Appendix: Proof of the upper bound

In this section, we prove Theorem 3.1. Suppose

$$f\left(\int a(y)c(z_i,y;r)p^+_{\alpha_1,\alpha_2}(y)\sigma_{n\setminus i}(dy)\right) \le \frac{e(z_i)p^+_{\alpha_1,\alpha_2}(z_i)}{1-p^+_{\alpha_1,\alpha_2}(z_i)} \tag{6.1}$$

for all $i=1,\dots,n$. Then $E_n(p^+_{\alpha_1,\alpha_2}(z))_i \le p^+_{\alpha_1,\alpha_2}(z_i)$ for all $i=1,\dots,n$. As E_n is monotone, the sequence of iterates of E_n starting from $p^+_{\alpha_1,\alpha_2}(z_i),\ i=1,\dots,n$ is decreasing. If T is primitive, then the cone limit set trichotomy [8, Theorem 6.3] holds and each sequence of iterates starting from a non-zero inital value must converge to p^*. Hence, $p^+_{\alpha_1,\alpha_2}(z_i),\ i=1,\dots,n$ is an upper bound on p^*. The matrix T is primitive with high probability by Lemma 5.5. It remains to show that for some $1/2<\alpha_2\le\alpha_1<1$ inequality (6.1) holds.

Since $c(z,y;r)=0$ for all y such that $\|y-z\|>r$, and since $p^+_{\alpha_1,\alpha_2}$ is Lipschitz with constant L_q, as given in (3.3), we have

$$\begin{aligned} f\left(\int a(y)c(z,y;r)p^+_{\alpha_1,\alpha_2}(y)\sigma_{n\setminus i}(dy)\right) &\le f\left(\int a(y)c(z,y;r)\left[p^+_{\alpha_1,\alpha_2}(z)+L_q r\right]\sigma_{n\setminus i}(dy)\right)\\ &\le f\left(\rho_{n\setminus i}(z)p^+_{\alpha_1,\alpha_2}(z)\right)+L_fL_q\rho_{n\setminus i}(z)r, \end{aligned} \tag{6.2}$$

for $\alpha_2>1/2$, where $\rho_{n\setminus i}(z) := \int a(y)c(z,y;r)\sigma_{n\setminus i}(dy)$.

U1. For all z such that $q_{\alpha_1}(z)<1-\alpha_2$,

$$\begin{aligned} &\frac{e(z)p^+_{\alpha_1,\alpha_2}(z)}{1-p^+_{\alpha_1,\alpha_2}(z)} - f\left(\int a(y)c(z,y;r)p^+_{\alpha_1,\alpha_2}(y)\sigma_{n\setminus i}(dy)\right)\\ &\ge \frac{e(z)(1-\alpha_2)}{\alpha_2} - f(\rho_n(z)(1-\alpha_2)) - L_fL_q\rho_{n\setminus i}(z)r\\ &\ge \frac{e(z)(1-\alpha_2)}{\alpha_2} - f(\rho(z)(1-\alpha_2)) - L_f((1-\alpha_2)+L_qr)\left|\rho(z)-\rho_{n\setminus i}(z)\right| - L_fL_q\rho(z)r. \end{aligned} \tag{6.3}$$

From Lemma 5.1, if $q_{\alpha_1}(z) \leq (1-\alpha_2)$, then $f(\rho(z)(1-\alpha_2)) \leq \alpha_1(1-\alpha_2)e(z)/\alpha_2$. Combining this bound with inequality (6.3) gives

$$
\begin{aligned}
&\frac{e(z)p^+_{\alpha_1,\alpha_2}(z)}{1-p^+_{\alpha_1,\alpha_2}(z)} - f\left(\int a(y)c(z,y;r)p^+_{\alpha_1,\alpha_2}(y)\sigma_{n\setminus i}(dy)\right) \\
&\geq \; \frac{e(z)(1-\alpha_1)(1-\alpha_2)}{\alpha_2} - L_f((1-\alpha_2)+L_q r)\left|\rho(z)-\rho_{n\setminus i}(z)\right| - L_f L_q \rho(z) r \\
&\geq \; p^+_{\alpha_1,\alpha_2}(z)\left(\frac{(1-\alpha_1)e(z)}{\alpha_2} - \frac{L_f L_q r\rho(z)}{p^+_{\alpha_1,\alpha_2}(z)} - L_f\left(1+\frac{L_q r}{p^+_{\alpha_1,\alpha_2}(z)}\right)\left|\rho(z)-\rho_{n\setminus i}(z)\right|\right), \quad (6.4)
\end{aligned}
$$

where the last inequality follows as $q_{\alpha_1}(z) < 1-\alpha_2$ implies $p^+_{\alpha_1,\alpha_2}(z) = 1-\alpha_2$.

U2. We now consider the case where $q_{\alpha_1}(z) \geq 1-\alpha_2$. Using the fact that $q_{\alpha_1}(z)$ is a fixed point of $F(\cdot;\rho(z),\alpha_1 e(z))$ and inequality (6.2), it follows that

$$
\begin{aligned}
&\frac{e(z)p^+_{\alpha_1,\alpha_2}(z)}{1-p^+_{\alpha_1,\alpha_2}(z)} - f\left(\int a(y)c(z,y;r)p^+_{\alpha_1,\alpha_2}(y)\sigma_{n\setminus i}(dy)\right) \\
&\geq \; \frac{f(\rho(z)q_{\alpha_1}(z))}{\alpha_1} - f(\rho_{n\setminus i}(z)q_\alpha(z)) - L_f L_q r \rho_{n\setminus i}(z) \\
&\geq \; \frac{(1-\alpha_1)}{\alpha_1} f(\rho(z)q_{\alpha_1}(z)) - L_f L_q r\rho(z) - L_f(q_\alpha(z)+L_q r)\left|\rho(z)-\rho_{n\setminus i}(z)\right|. \quad (6.5)
\end{aligned}
$$

Since $f(\rho(z)q_{\alpha_1}(z)) = \alpha_1 e(z)q_{\alpha_1}(z)/(1-q_{\alpha_1}(z)) \geq \alpha_1 e(z)q_{\alpha_1}(z)$ and $q_{\alpha_1}(z) \geq 1-\alpha_2$ here, inequality (6.5) becomes

$$
\begin{aligned}
&\frac{e(z)p^+_{\alpha_1,\alpha_2}(z)}{1-p^+_{\alpha_1,\alpha_2}(z)} - f\left(\int a(y)c(z,y;r)p^+_{\alpha_1,\alpha_2}(y)\sigma_{n\setminus i}(dy)\right) \\
&\geq \; q_{\alpha_1}(z)\left((1-\alpha_1)e(z) - \frac{L_f L_q r\rho(z)}{q_{\alpha_1}(z)} - L_f\left(1+\frac{L_q r}{q_{\alpha_1}(z)}\right)\left|\rho(z)-\rho_{n\setminus i}(z)\right|\right) \\
&\geq \; p^+_{\alpha_1,\alpha_2}(z)\left((1-\alpha_1)e(z) - \frac{L_f L_q r\rho(z)}{p^+_{\alpha_1,\alpha_2}(z)} - L_f\left(1+\frac{L_q r}{p^+_{\alpha_1,\alpha_2}(z)}\right)\left|\rho(z)-\rho_{n\setminus i}(z)\right|\right). \quad (6.6)
\end{aligned}
$$

U3. Combining inequalities (6.4) and (6.6), we see that inequality (6.1) holds if

$$
(1-\alpha_1)e(z_i) - \frac{L_f L_q r\rho(z_i)}{p^+_{\alpha_1,\alpha_2}(z_i)} - L_f\left(1+\frac{L_q r}{p^+_{\alpha_1,\alpha_2}(z_i)}\right)\left|\rho(z_i)-\rho_{n\setminus i}(z_i)\right| \geq 0
$$

which is equivalent to

$$
\frac{(1-\alpha_1)e(z_i)p^+_{\alpha_1,\alpha_2}(z_i) - L_f L_q r\rho(z_i)}{L_f\left(p^+_{\alpha_1,\alpha_2}(z_i)+L_q r\right)} \;\geq\; \left|\rho(z_i)-\rho_{n\setminus i}(z_i)\right|.
$$

By Lemma 5.3, $p^+_{\alpha_1,\alpha_2}(z) \geq \left(\alpha_1\eta_\Omega \vee (1-\alpha_2)\right)$, and from inequality (3.2) together with $L_f\rho_{\max}/e_{\min} > 1/2$, we see that inequality (6.1) is satisfied if

$$
\frac{(1-\alpha_1)e_{\min}}{4L_f} \;\geq\; \left|\rho(z_i)-\rho_{n\setminus i}(z_i)\right|.
$$

Applying Lemma 5.4 yields the bound

$$\begin{aligned}
&\mathbb{P}\left(\max_i \left| \int a(y)c(z_i,y;r)[\sigma_{n\setminus i}(dy) - \sigma(y)\,dy]\right| \le \frac{(1-\alpha_1)e_{\min}}{4L_f}\right) \\
&\ge\ 1 - n\sup_{z\in\Omega}\mathbb{P}\left(\left| \int a(y)c(z,y;r)[\sigma_{n\setminus i}(dy) - \sigma(y)\,dy]\right| > \frac{(1-\alpha_1)e_{\min}}{4L_f}\right) \\
&\ge\ 1 - 2n\exp\left(-C_2\{(n-1)r^d/A\}\frac{e_{\min}^2(1-\alpha_1)^2}{16a_{\max}^2L_f^2}\right),
\end{aligned}$$

if $\frac{(1-\alpha_1)e_{\min}}{4L_f} \le \rho_{\max}$, which is the case if $L_f\rho_{\max}/e_{\min} > 1/2$.

The situation in which $L_f\rho_{\max}/e_{\min} \le 1/2$ is one in which the metapopulation is nowhere viable, so the conclusion is not surprising. We begin by noting that $q_\alpha(z) = 0$ for all $\alpha > 1/2$ if $L_f\rho_{\max}/e_{\min} \le 1/2$, so that $p^+_{\alpha_1,\alpha_2}(z) = (1-\alpha_2)$ for all $z \in \Omega$. Lemma 5.4 with $t = \rho_{\max}/2$ then shows that

$$\left|\rho(z_i) - \rho_{n\setminus i}(z_i)\right| \ \le\ \frac{1}{2}\rho_{\max},$$

on an event of probability at least

$$1 - 2\exp\left\{-C_2\frac{(n-1)r^d}{A}\left(\frac{\rho_{\max}}{2a_{\max}}\right)^2\right\}.$$

Hence, on this event, we have

$$f\left((1-\alpha_2)\int a(y)c(z_i,y;r)\sigma_{n\setminus i}(dy)\right) \ \le\ \frac{3}{2}(1-\alpha_2)L_f\rho_{\max} \ \le\ (1-\alpha_2)e_{\min} \ \le\ \frac{e(z_i)(1-\alpha_2)}{\alpha_2}.$$

This establishes (6.1), on an event with probability as given in Theorem 3.1, for any choice of $1/2 < \alpha_2 < 1$, since $p^+_{\alpha_1,\alpha_2}(z) = (1-\alpha_2)$ for all $z \in \Omega$. This completes the proof of Theorem 3.1.

7. Appendix: Proof of the lower bound

To find a good lower bound on p^*_n, we introduce a modification of E_n. For any $\Theta \subseteq \Omega$ and $\beta > 1$ define the operator $E_{n,\Theta,\beta} : [0,1]^n \to [0,1]^n$ by

$$E_{n,\Theta,\beta}(p)_i \ :=\ \frac{f\left((A/(n-1))\sum_{j\ne i} a(z_j)c(z_i,z_j;r)\mathbb{I}(z_j\in\Theta)p_j\right)}{\beta e(z_i) + f\left((A/(n-1))\sum_{j\ne i} a(z_j)c(z_i,z_j;r)\mathbb{I}(z_j\in\Theta)p_j\right)}.$$

Denote the largest fixed point of $E_{n,\Theta,\beta}$ by $p^*_{n,\Theta,\beta}$. Since f is an increasing function, for any $\Theta \subseteq \Omega$ and any $\beta > 1$, $E_{n,\Theta,\beta}(p) \le E_{n,\Theta,1}(p) \le E_n(p)$ for all $p \in [0,1]^n$, which implies that $p^*_{n,\Theta,\beta} \le p^*_{n,\Theta,1} \le p^*_n$. Thus a lower bound on $p^*_{n,\Theta,\beta}$ yields a lower bound on p^*_n. To construct a lower bound on $p^*_{n,\Theta,\beta}$, we examine the limiting form of $E_{n,\Theta,\beta}$ as $n \to \infty$. Let $C^+(\Theta)$ be the set of non-negative functions on Θ and define $E_{\Theta,\beta}\colon\ C^+(\Theta) \to C^+(\Theta)$ by

$$E_{\Theta,\beta}(p) \ := \ \frac{f\left(\int a(y)c(z,y;r)\mathbb{I}(y \in \Theta)p(y)\sigma(dy)\right)}{\beta e(z) + f\left(\int a(y)c(z,y;r)\mathbb{I}(y \in \Theta)p(y)\sigma(dy)\right)}.$$

Let $p^*_{\Theta,\beta}$ denote the largest fixed point of $E_{\Theta,\beta}$. Our aim now is to find a $\beta > 1$ such that with high probability

$$p^*_{i,n} \ \geq \ p^*_{\Theta,\beta}(z_i), \tag{7.1}$$

for all $z_i \in \Theta$.

Lemma 7.1. *Suppose that Assumptions A, B, D and E hold. Suppose also that, for a given $\Theta \subseteq \Omega$ and $\beta > 1$, there exists an $\epsilon_{\Theta,\beta} > 0$ such that $p^*_{\Theta,\beta}(z) \geq \epsilon_{\Theta,\beta}$ for all $z \in \Theta$. Assume that*

$$e_{\min}\epsilon_{\Theta,\beta}(\beta - 1) \ \leq \ L_f \rho_{\max}. \tag{7.2}$$

Then

$$\mathbb{P}\left(p^*_{i,n} \geq p^*_{\Theta,\beta}(z_i) \text{ for all } z_i \in \Theta\right) \ \geq \ 1 - 2n \exp\left(-C_2 \frac{(n-1)r^d}{A} \frac{e^2_{\min}\epsilon^2_{\Theta,\beta}(\beta-1)^2}{4a^2_{\max}L^2_f}\right). \tag{7.3}$$

Proof. Suppose that

$$\frac{e(z_i)p^*_{\Theta,\beta}(z_i)}{1 - p^*_{\Theta,\beta}(z_i)} \ \leq \ f\left(\int a(y)c(z_i,y;r)\mathbb{I}(y \in \Theta)p^*_{\Theta,\beta}(y)\sigma_{n\setminus i}(dy)\right) \tag{7.4}$$

for all $z_i \in \Theta$. Then $E_{n,\Theta,1}$ maps the set $\{p : p^*_{\Theta,\beta}(z_i) \leq p_i \leq 1\}$ into itself as the map is monotone. Applying the Brouwer fixed point theorem, we see $p^*_{\Theta,\beta}(z_i) \leq p_{n,\Theta,1,i}$ for all $z_i \in \Theta$. Since $p^*_{n,\Theta,1} \leq p^*_n$, it remains to verify inequality (7.4) holds.

Now

$$
\begin{aligned}
& f\left(\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)\sigma_{n\backslash i}(dy)\right)\\
&= f\biggl(\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)\sigma(y)\,dy\\
&\qquad + \int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)[\sigma_{n\backslash i}(dy)-\sigma(y)\,dy]\biggr)\\
&\geq f\biggl(\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)\sigma(y)\,dy\biggr)\\
&\qquad - L_f\left|\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)[\sigma_{n\backslash i}(dy)-\sigma(y)\,dy]\right|\\
&\geq \frac{\beta e(z_i)p^*_{\Theta,\beta}(z_i)}{1-p^*_{\Theta,\beta}(z_i)} - L_f\left|\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)[\sigma_{n\backslash i}(dy)-\sigma(y)\,dy]\right|.
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
& f\left(\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)\sigma_{n\backslash i}(dy)\right) - \frac{e(z_i)p^*_{\Theta}(z_i)}{1-p^*_{\Theta,\beta}(z_i)}\\
&\geq \frac{(\beta-1)e(z_i)p^*_{\Theta,\beta}(z_i)}{1-p^*_{\Theta,\beta}(z_i)} - L_f\left|\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)[\sigma_{n\backslash i}(dy)-\sigma(y)\,dy]\right|.
\end{aligned}
$$

As $p^*_\Theta(z)\geq \epsilon_{\Theta,\beta}$ for all $z\in\Theta$, inequality (7.1) will hold if

$$
\frac{(\beta-1)e_{\min}\epsilon_{\Theta,\beta}}{L_f} - \left|\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)[\sigma_{n\backslash i}(dy)-\sigma(y)\,dy]\right| \;\geq\; 0, \tag{7.5}
$$

for all $z_i\in\Theta$. Applying Lemma 5.4 yields the bound

$$
\begin{aligned}
& \mathbb{P}\left(\max_{i:z_i\in\Theta}\left|\int a(y)c(z_i,y;r)\mathbb{I}(y\in\Theta)p^*_{\Theta,\beta}(y)[\sigma_{n\backslash i}(dy)-\sigma(y)\,dy]\right| > \frac{e_{\min}\epsilon_{\Theta,\beta}(\beta-1)}{L_f}\right)\\
&\leq 2n\exp\left(-C_2\frac{(n-1)r^d}{A}\frac{e^2_{\min}\epsilon^2_{\Theta,\beta}(\beta-1)^2}{a^2_{\max}L_f^2}\right),
\end{aligned}
$$

if inequality (7.2) holds. □

Lemma 7.1 shows that inequality (7.1) holds with high probability if $p^*_{\Theta,\beta}$ can be bounded away from zero. We now establish a lower bound on $p^*_{\Theta,\beta}$.

To state the lemma that we need, some further notation is necessary. With $\Theta := \Theta_{x,t}$ as before, suppose that $\eta_\Theta := \inf_{z\in\Theta} q_1(z) > 0$. Recall C_1, as introduced following Assumption E, and set

$$
c_\Theta \;:=\; \inf_{z\in\Theta}\int_0^1 c_z(\lambda)\lambda^d\,d\lambda; \tag{7.6}
$$

$$
C_3 \;:=\; v_d c_{\max}(a_{\max}L_\sigma + \sigma_{\max}L_a). \tag{7.7}
$$

Lemma 7.2. *Suppose that Assumptions B–E hold. Define*

$$q_{\Theta,\beta',m}(z) := (m(t - \|z - x\|) \wedge q_{\beta'}(z))\,.$$

If there exists constants $\beta' \in (\beta, (1-\eta_\Theta)^{-1})$, $\theta_1 \in (1,\infty)$, $\theta_2 \in (0,1)$ *and* $m \in (0,\infty)$ *such that*

$$(1+\theta_1)mr \;\le\; (\beta'\eta_\Theta + 1 - \beta'); \tag{7.8}$$

$$L_f\rho_{\max}(m \vee L_q)r \;\le\; (\beta' - \beta)e_{\min}\theta_1 mr; \tag{7.9}$$

$$\frac{L_f(C_3 + \rho_{\max}/t)r}{\theta_2} + \rho_{\max}(C_1\rho_{\max} + L_f)\theta_1 mr \;\le\; e_{\min}(\beta\eta_\Theta + 1 - \beta); \tag{7.10}$$

$$\frac{r}{t} \;\le\; \min\Big\{\theta_2, \frac{1}{2(2+\theta_1)}\Big\}; \tag{7.11}$$

$$(C_3 + \rho_{\max}/t)r \;\le\; a_{\min}v_{d-1}\sigma_{\min}\left(c_\Theta - 2c_{\max}\theta_2\right)(1-\theta_2^2)^{(d-1)/2}, \tag{7.12}$$

then $q_{\Theta,\beta',m}(z) \le p^*_{\Theta,\beta}(z)$ *for all* $z \in \Theta$.

Proof. Suppose that

$$\frac{\beta e(z)q_{\Theta,\beta',m}(z)}{1 - q_{\Theta,\beta',m}(z)} \;\le\; f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y \in \Theta)\sigma(y)\,dy\right) \tag{7.13}$$

for all $z \in \Theta$. Then $E_{\Theta,\beta}$ maps $\{p \in C^+(\Theta) : q_{\Theta,\beta',m} \le p\}$ into itself. The map $E_{\Theta,\beta}$ is compact by Assumption C. By the Schauder fixed point theorem, $q_{\Theta,\beta',m} \le p^*_{\Theta,\beta}$. We now verify that inequality (7.13) holds.

L1.For any z such that $\|z - x\| \le t - r$,

$$\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y \in \Theta)\sigma(y)\,dy \;=\; \int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\sigma(y)\,dy.$$

From Lemma 5.2, $q_{\Theta,\beta',m}$ is Lipschitz continuous with constant $(m \vee L_q)$. Hence,

$$\begin{aligned}
&f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y \in \Theta)\sigma(y)\,dy\right)\\
&= f\left(q_{\Theta,\beta',m}(z)\int a(y)c(z,y;r)\sigma(y)\,dy + \int a(y)c(z,y;r)[q_{\Theta,\beta',m}(y) - q_{\Theta,\beta',m}(z)]\sigma(y)\,dy\right)\\
&\ge f\left(\rho(z)q_{\Theta,\beta',m}(z)\right) - L_f\rho(z)(m \vee L_q)r.
\end{aligned} \tag{7.14}$$

As $q_{\Theta,\beta',m}(z) \le q_{\beta'}(z)$, we can apply Lemma 5.1 with inequality (7.14) to show

$$\begin{aligned} f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy\right) - \frac{\beta e(z) q_{\Theta,\beta',m}(z)}{1-q_{\Theta,\beta',m}(z)} \\ \ge \frac{(\beta'-\beta)e(z)q_{\Theta,\beta',m}(z)}{1-q_{\Theta,\beta',m}(z)} - L_f\rho(z)(m\vee L_q)r. \end{aligned} \tag{7.15}$$

From the definition of η_Θ, $q_{\beta'}(z) \ge (\beta'\eta_\Theta + 1 - \beta')$ for all $z\in\Theta$, by Lemma 5.3. Set $\Theta_1 := \{y : \|y-x\| \le t-\theta_1 r\}$. Then $q_{\Theta,\beta',m}(z) \ \ge\ \theta_1 mr$ for all $z \in \Theta_1$ by inequality (7.8). Applying this lower bound to inequality (7.15), we see that inequality (7.13) holds for all $z\in\Theta_1$ if inequality (7.9) holds.

L2. Define $\Theta_2 := \{y : t-\theta_1 r < \|y-x\| \le t-\theta_2 r\}$. For any $z\in\Theta_2$ and y such that $\|y-z\|\le r$,

$$m(t-\|y-x\|) \ \le\ m(t-\|z-x\|+\|z-y\|) \ \le\ (1+\theta_1)mr \ \le\ q_{\beta'}(y)$$

by Lemma 5.3 and since $(1+\theta_1)mr \le \beta'\eta_\Theta + 1-\beta'$ by inequality (7.8). Therefore, for any $z\in\Theta_2$ and $y\in\Theta$ such that $\|y-z\|\le r$, $q_{\Theta,\beta',m}(y) = m(t-\|y-x\|)$. For any $z\in\Theta_2$ and $y\notin\Theta$ such that $\|y-z\|\le r$, we have $m(t-\|y-x\|)\le 0$. Hence

$$\begin{aligned} &\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy \\ &\quad\ge \int a(y)c(z,y;r)m(t-\|y-x\|)\sigma(y)\,dy \\ &\quad= m(t-\|z-x\|)\rho(z) + m\int a(y)c(z,y;r)\left[\|z-x\|-\|y-x\|\right]\sigma(y)\,dy. \end{aligned} \tag{7.16}$$

Let $\gamma(x,y,z)$ be the angle formed between the vectors $x-z$ and $y-z$. By the cosine rule

$$\begin{aligned} &\|z-x\|-\|y-x\|-\|z-y\|\cos\gamma(x,y,z) \\ &\quad= \|z-x\|\left(1-\left(1+\left(\frac{\|z-y\|}{\|z-x\|}\right)^2 - 2\left(\frac{\|z-y\|}{\|z-x\|}\right)\cos\gamma(x,y,z)\right)^{1/2}\right) - \|z-y\|\cos\gamma(x,y,z). \end{aligned}$$

Let $h(u) = (1+u^2-2u\cos\gamma)^{1/2}$. Taking a Taylor expansion about 0 gives $h(u) = 1 - u\cos\gamma + \frac{1}{2}u^2 h''(\tilde{u})$ for some $\tilde{u} \in (0,u)$. Therefore,

$$\begin{aligned}
&\|z-x\| - \|y-x\| - \|z-y\|\cos\gamma(x,y,z) \\
&\geq\ -\frac{\|z-y\|^2}{2\|z-x\|} \sup_{\xi\in(0,\frac{\|z-y\|}{\|z-x\|})} \left(1+\xi^2-2\xi\cos\gamma(x,y,z)\right)^{-1/2} \\
&\geq\ -\frac{r^2}{2\|z-x\|}\left(1-\frac{2r}{\|z-x\|}\right)^{-1}.
\end{aligned}$$

Noting that $\|z-x\| \geq t - \theta_1 r$ and substituting this bound into (7.16) gives

$$\begin{aligned}
&\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy \\
&\quad\geq\ q_{\Theta,\beta',m}(z)\rho(z) + m\int a(y)c(z,y;r)\|z-y\|\cos\gamma(x,y,z)\sigma(y)\,dy - \frac{mr^2\rho(z)}{2(t-(2+\theta_1)r)},
\end{aligned}$$

if $t > (2+\theta_1)r$; but this follows from inequality (7.11), which gives $t-(2+\theta_1)r \geq t/2$. Now, from Assumption C,

$$\begin{aligned}
&\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy \\
&\quad\geq\ q_{\Theta,\beta',m}(z)\rho(z) + ma(z)\sigma(z)\int c(z,y;r)\|z-y\|\cos\gamma(x,y,z)dy \\
&\qquad + ma(z)\int c(z,y;r)\|z-y\|\cos\gamma(x,y,z)[\sigma(y)-\sigma(z)]dy \\
&\qquad + m\int [a(y)-a(z)]c(z,y;r)\|z-y\|\cos\gamma(x,y,z)\sigma(y)dy - \frac{mr^2\rho(z)}{t} \\
&\quad\geq\ q_{\Theta,\beta',m}(z)\rho(z) + ma(z)\sigma(z)\int c(z,y;r)\|z-y\|\cos\gamma(x,y,z)dy - (C_3+\rho_{\max}/t)mr^2.
\end{aligned} \tag{7.17}$$

By the radial symmetry of $c(z,y;r)$, $\int c(z,y;r)\|z-y\|\cos\gamma(x,y,z)dy = 0$. Thus we deduce that

$$f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\sigma(y)\,dy\right)\ \geq\ f\left(q_{\Theta,\beta',m}(z)\rho(z)\right) - L_f(C_3+\rho_{\max}/t)mr^2.$$

Therefore, applying Lemma 5.1 and noting that $f(x) \geq L_f x - C_1 x^2$ gives

$$\begin{aligned}
& f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\sigma(y)\,dy\right) - \frac{\beta e(z)q_{\Theta,\beta',m}(z)}{1-q_{\Theta,\beta',m}(z)} \\
& \geq\ f\left(q_{\Theta,\beta',m}(z)\rho(z)\right) - \frac{\beta e(z)q_{\Theta,\beta',m}(z)}{1-q_{\Theta,\beta',m}(z)} - L_f(C_3+\rho_{\max}/t)mr^2 \\
& \geq\ \frac{q_{\Theta,\beta',m}(z)}{1-q_{\Theta,\beta',m}(z)}\left(L_f\rho(z)(1-q_{\Theta,\beta',m}(z)) - \beta e(z) - \frac{L_f(C_3+\rho_{\max}/t)mr^2}{q_{\Theta,\beta',m}(z)} - C_1\rho^2(z)q_{\Theta,\beta',m}(z)\right) \\
& \geq\ \frac{q_{\Theta,\beta',m}(z)}{1-q_{\Theta,\beta',m}(z)}\left(L_f\rho(z) - \beta e(z) - \frac{L_f(C_3+\rho_{\max}/t)mr^2}{q_{\Theta,\beta',m}(z)} - \rho(z)q_{\Theta,\beta',m}(z)(C_1\rho(z)+L_f)\right)
\end{aligned} \tag{7.18}$$

We now need a lower bound on $L_f\rho(z) - \beta e(z)$. By Assumption E, we have

$$(1-q_\beta(z))L_f\rho(z)q_\beta(z)\ \geq\ \beta e(z)q_\beta(z).$$

Hence, because $L_f\rho(z) > e(z)$ whenever $q_1(z) > 0$, we deduce that

$$L_f\rho(z) - \beta e(z)\ \geq\ L_f\rho(z)q_\beta(z)\ \geq\ e(z)q_\beta(z).$$

This, together with the lower bound on $q_\beta(z)$ from Lemma 5.3, gives $L_f\rho(z) - \beta e(z) \geq e_{\min}(\beta\eta_\Theta + 1 - \beta)$. As $\theta_2 mr \leq q_{\Theta,\beta',m}(z) \leq \theta_1 mr$ for all $z \in \Theta_2$ we see that the right hand side of inequality (7.18) is positive if inequality (7.10) holds. Hence, inequality (7.13) holds for all $z \in \Theta_2$.

L3. Define $\Theta_3 := \{y : t - \theta_2 r < \|y-x\| \leq t\}$. As in **L2**, for any $z \in \Theta_3$ and y such that $\|y-z\| \leq r$, we have $q_{\Theta,\beta',m}(y) = m(t - \|y-x\|)$. Following inequality (7.17) in **L2**,

$$\begin{aligned}
& \int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy - m(t-\|z-x\|)\rho(z) \\
& \quad \geq\ ma(z)\sigma(z)\int c(z,y;r)\|z-y\|\cos\gamma(x,y,z)\mathbb{I}(y\in\Theta)dy - (C_3+\rho_{\max}/t)mr^2.
\end{aligned}$$

As $\theta_2 < 1$, let w be a point of intersection of the ball $B_z(r)$ with $\partial\Theta$, and let $\phi := \gamma(x,w,z)$. Applying the change of variable $\lambda(y) = r^{-1}\|z-y\|$ and $\omega(y) = \gamma(x,y,z)$ yields

$$\int_{\{y:-\phi\leq\omega(y)\leq\phi\}} c(z,y;r)\|z-y\|\cos\omega(y)\mathbb{I}(y\in\Theta)dy\ \geq\ v_{d-1}r\left(\int_0^1 c_z(\lambda)\lambda^d\,d\lambda\right)(\sin\phi)^{d-1}.$$

It remains to determine a lower bound for the integral

$$\int_{\{y:\gamma(x,y,z)\in[-\pi,-\phi)\cup(\phi,\pi]\}} c(z,y;r)\|z-y\|\cos\gamma(x,y,z)\mathbb{I}(y\in\Theta)\,dy. \tag{7.19}$$

The region of integration is included in a cylinder of height $(t-\|z-x\|)+r\max\{\cos\phi,0\}$ and radius $r\sin\phi$. As ϕ is determined by the intersection of two circles,

$$\cos\phi \;=\; r^{-1}\left(\|z-x\| - \frac{\|z-x\|^2 - r^2 + t^2}{2\|z-x\|}\right) \;=\; \frac{\|z-x\|-t}{r} + \frac{r[1-((t-\|z-x\|)/r)^2]}{2\|z-x\|}.$$

The function $x + r(1-x^2)/(2(t+rx))$ is increasing when $t > r$, and so

$$-\theta_2 \;\le\; \cos\phi \;\le\; \frac{r}{2t}. \tag{7.20}$$

Hence, for $z \in \Theta_3$, the volume of integration cannot exceed

$$v_{d-1}(r\sin\phi)^{d-1}(\theta_2 r + r^2/t) \;\le\; 2v_{d-1}(r\sin\phi)^{d-1}\theta_2 r,$$

by inequality (7.11). The largest negative value of the integrand is bounded below by $-c_{\max}r^{-d+1}$. Hence this integral is bounded below by $-2c_{\max}v_{d-1}r(\sin\phi)^{d-1}\theta_2$. This leads to the lower bound

$$\begin{aligned}
&\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy - m(t-\|z-x\|)\rho(z) \\
&\quad\ge\; mra(z)\sigma(z)v_{d-1}\left(c_\Theta - 2c_{\max}\theta_2\right)(\sin\phi)^{d-1} - (C_3+\rho_{\max}/t)mr^2.
\end{aligned} \tag{7.21}$$

From inequalities (7.11) and (7.20), $(\sin\phi)^{d-1} \;\ge\; (1-\theta_2^2)^{(d-1)/2}$. Applying inequality (7.12), we see that the right-hand side of (7.21) is positive. Therefore,

$$f(\rho(z)q_{\Theta,\beta',m}(z)) \;\le\; f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy\right).$$

Lemma 5.1, with $\tau = \rho(z)$ and $\nu = \beta' e(z)$, then implies that inequality (7.13) holds for all $z \in \Theta_3$. Hence, $q_{\Theta,\beta',m}(z) \le p^*_{\Theta,\beta}(z)$ for all $z \in \Theta$.

□

Lemma 7.3. *Suppose that Assumptions B–E hold, that* $\inf_{z\in\Omega} q_1(z) =: \eta_\Theta > 0$ *and that* $\beta \in (1, 1+\eta_\Theta/2)$. *Assume that*

$$L_q r \;\le\; \frac{\eta_\Theta^2 e_{\min}^2}{32L_f\rho_{\max}^2(C_1\rho_{\max}+L_f)}; \tag{7.22}$$

$$\frac{r}{t} \;\le\; \left(\frac{c_\Theta}{4c_{\max}} \wedge \frac{1}{\sqrt{2}} \wedge \frac{\eta_\Theta e_{\min}}{8L_f\rho_{\max} + 4\eta_\Theta e_{\min}}\right); \tag{7.23}$$

$$(C_3+\rho_{\max}/t)r \;\le\; \left\{a_{\min}\sigma_{\min}c_\Theta v_{d-1}2^{-(d+3)/2}\right\} \wedge \left\{\frac{\eta_\Theta e_{\min}}{4L_f}\left(\frac{c_\Theta}{4c_{\max}} \wedge \frac{1}{\sqrt{2}}\right)\right\}, \tag{7.24}$$

and define

$$C_4 \;:=\; \left(1 \wedge \frac{f(a_{\min}\sigma_{\min})}{2^{(d+1)/2}e_{\max}}\right)\left(\frac{c_\Theta}{4c_{\max}} \wedge \frac{1}{\sqrt{2}}\right)\frac{e_{\min}^2}{32L_f\rho_{\max}^2(C_1\rho_{\max}+L_f)}. \tag{7.25}$$

Then $p^*_{\Theta,\beta}(z) \geq C_4\eta_\Theta^2$ *for all* $z \in \Theta$.

Proof. We begin by showing that the above inequalities are sufficient for the inequalities of Lemma 7.2 to hold, for suitable choices of $\beta', \theta_1, \theta_2$ and m. Set $\beta' = \frac{1}{2(1-\eta_\Theta)} + \frac{\beta}{2}$. Then

$$\beta' - \beta \;=\; \frac{1}{2(1-\eta_\Theta)} - \frac{\beta}{2} = \frac{\beta\eta_\Theta + 1 - \beta}{2(1-\eta_\Theta)} \;\geq\; \frac{\eta_\Theta(1+\eta_\Theta)}{4(1-\eta_\Theta)} \;\geq\; \frac{\eta_\Theta}{4}, \tag{7.26}$$

and

$$\beta'\eta_\Theta + 1 - \beta' \;=\; \frac{1}{2}(\beta\eta_\Theta + 1 - \beta) \;\geq\; \frac{\eta_\Theta}{4}. \tag{7.27}$$

Set

$$\begin{aligned} \theta_1 \;&:=\; \frac{4L_f\rho_{\max}}{\eta_\Theta e_{\min}}; \\ mr \;&:=\; \frac{\eta_\Theta^2 e_{\min}^2}{32L_f\rho_{\max}^2(C_1\rho_{\max}+L_f)}; \\ \theta_2 \;&:=\; \left(\frac{c_\Theta}{4c_{\max}} \wedge \frac{1}{\sqrt{2}}\right). \end{aligned}$$

Since

$$\frac{L_f\rho_{\max}}{\eta_\Theta e_{\min}} \;\geq\; \frac{L_f\rho(z)}{\eta_\Theta e(z)} \;\geq\; \frac{1+q_1(z)}{\eta_\Theta} \;\geq\; \frac{1+\eta_\Theta}{\eta_\Theta} \;\geq\; 1,$$

it follows that $\theta_1 > 1$. This, together with inequality (7.27), implies that inequality (7.8) is satisfied if $8\theta_1 mr \leq \eta_\Theta$. This is indeed the case, since, from the choices of θ_1 and mr, we have

$$8\theta_1 mr \;\leq\; \eta_\Theta\,\frac{e_{\min}}{L_f\rho_{\max}} \;\leq\; \eta_\Theta,$$

because $L_f\rho_{\max}/e_{\min} > 1$ if $\eta_\Theta > 0$.

Then $L_q r \leq mr$, by inequality (7.22), so inequality (7.9) simplifies to give $L_f\rho_{\max} \leq (\beta' - \beta)e_{\min}\theta_1$; and this is seen to hold, by inequality (7.26) and the choice of θ_1. The choices of θ_1 and θ_2, together with inequality (7.27), show further that inequality (7.10) is implied by inequality (7.24), and that inequality (7.11) is implied by inequality (7.23). Finally, the choice of θ_2 shows that inequality (7.12) follows from inequality (7.24). Thus, inequalities (7.8)–(7.12) in Lemma 7.2 hold.

Take Θ_1, Θ_2 and Θ_3 as defined in the proof of Lemma 7.2. On $\Theta_1 \cup \Theta_2$,

$$p^*_{\Theta,\beta}(z) \;\geq\; q_{\Theta,\beta',m}(z) \;\geq\; \theta_2 mr.$$

For $z \in \Theta_3$, note that $q_{\Theta,\beta',m} \le E_{\Theta,\beta}(q_{\Theta,\beta',m}) \le p^*_{\Theta,\beta}$ and that

$$E_{\Theta,\beta}(q_{\Theta,\beta',m})(z) \;\ge\; \frac{f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy\right)}{\beta e(z)}.$$

Now inequalities (7.21) and (7.24) imply that

$$f\left(\int a(y)c(z,y;r)q_{\Theta,\beta',m}(y)\mathbb{I}(y\in\Theta)\sigma(y)\,dy\right) \;\ge\; f\left(mr\,\frac{a_{\min}\sigma_{\min}c_\Theta}{2^{(d+3)/2}c_{\max}}\right) \;\ge\; f\left(\theta_2 mr\,\frac{a_{\min}\sigma_{\min}}{2^{(d-1)/2}}\right).$$

Then, from Assumption E, we have $f(ab) \ge bf(a)$ if $0 \le b \le 1$. Now $\theta_2 < 1$, $2^{(d-1)/2} \ge 1$ and $mr \le 1/32$, because $0 < \eta_\Theta \le 1$ and $L_f\rho_{\max}/e_{\min} > 1$, so we conclude that

$$p^*_{\Theta,\beta}(z) \;\ge\; \frac{f\left(a_{\min}\sigma_{\min}\right)}{2^{(d-1)/2}}\,\theta_2 mr\,\frac{1}{\beta e_{\max}} \;\ge\; \frac{f\left(a_{\min}\sigma_{\min}\right)}{2^{(d+1)/2}e_{\max}}\,\theta_2 mr$$

for all $z \in \Theta_3$.

Combining this with the lower bound on $q_{\Theta,\beta',m}$ for $z \in \Theta_1 \cup \Theta_2$ gives the uniform lower bound. □

Lemma 7.4. *Suppose that Assumptions B–E hold, that* $\inf_{z\in\Omega} q_1(z) =: \eta_\Theta > 0$ *and that* $1 < \beta < \beta' < 1 + \eta_\Theta/2$. *Assume that, in addition to inequalities (7.23)–(7.24),*

$$L_q r \;\le\; \frac{e_{\min}^2\eta_\Theta(\beta'-\beta)}{4\rho_{\max}^2 L_f(C_1\rho_{\max}+L_f)}; \tag{7.28}$$

$$\frac{r}{t} \;\le\; \frac{e_{\min}(\beta'-\beta)}{6L_f\rho_{\max}}. \tag{7.29}$$

Then, choosing m as in Theorem 3.2 so that

$$mr \;=\; \frac{e_{\min}^2\eta_\Theta(\beta'-\beta)}{4\rho_{\max}^2 L_f(C_1\rho_{\max}+L_f)},$$

it follows that $p^*_{\Theta,\beta}(z) \ge q_{\Theta,\beta',m}(z)$ for all $z \in \Theta$.

Proof. We show that the above inequalities are sufficient for the inequalities of Lemma 7.2 to hold, with suitable choices of θ_1 and θ_2. Set

$$\theta_1 \;:=\; \frac{L_f\rho_{\max}}{e_{\min}(\beta'-\beta)},$$

and choose θ_2 as in Lemma 7.3. Note that $\theta_1 > 1$, since $\beta'-\beta \le 1 \le L_f\rho_{\max}/e_{\min}$. Since $\beta'\eta_\Theta + 1 - \beta' \ge \eta_\Theta/2$, inequality (7.8) holds if $4mr \le \eta_\Theta$; but this is true with the above choice of mr, because $(\beta'-\beta) < 1$ and $L_f\rho_{\max}/e_{\min} > 1$.

From inequality (7.28), $L_q r \le mr$, and so inequality (7.9) simplifies to give $L_f\rho_{\max} \le (\beta'-\beta)e_{\min}\theta_1$, which holds with equality for θ_1 as chosen. To show that inequality (7.10) holds, we first note that $4\rho_{\max}(C_1\rho_{\max} + L_f)\theta_1 mr \leq e_{\min}\eta_\Theta$. Therefore, inequality (7.10) holds if $4L_f(C_3 + \rho_{\max}/t)r \leq \theta_2 e_{\min}\eta_\Theta$, which follows from inequality (7.24).

The second part of inequality (7.11) holds by (7.29) and because

$$2(2+\theta_1) \;=\; \frac{4e_{\min}(\beta'-\beta) + 2L_f\rho_{\max}}{e_{\min}(\beta'-\beta)} \;\leq\; \frac{6L_f\rho_{\max}}{e_{\min}(\beta'-\beta)},$$

again since $\beta' - \beta \leq 1 \leq L_f\rho_{\max}/e_{\min}$.

Finally, with θ_2 chosen as in Lemma 7.3, inequality (7.12) follows from (7.24) as in Lemma 7.3, and the first part of inequality (7.11) follows from (7.23).

□

Proof of Theorem 3.2. First note that inequality (7.2) of Lemma 7.1 holds with $\epsilon_{\Theta,\beta} = C_4\eta_\Theta^2$, since

$$C_4 \;\leq\; \frac{e_{\min}^2}{32\sqrt{2}L_f^2\rho_{\max}^2} \;\leq\; \frac{1}{8\sqrt{2}}$$

when $L_f\rho_{\max}/e_{\min} > 1/2$, and hence

$$C_4\eta_\Theta^2(\beta-1) \;\leq\; C_4\frac{\eta_\Theta^3}{2} \;\leq\; \frac{1}{16\sqrt{2}} \;<\; \frac{1}{2} \;\leq\; \frac{L_f\rho_{\max}}{e_{\min}}.$$

Now combine Lemmas 7.1, 7.3 and 7.4. □

Proof of Corollary 3.3. By Theorem 3.1, $p_{i,n}^* \leq p_{\alpha_1,\alpha_2}^+(z_i)$ for all $i = 1,\ldots,n$ with high probability. Taking $\alpha_2 = 1 - \eta_\Theta$, we note that $q_{\alpha_1}(z) \geq q_1(z) \geq \eta_\Theta$, and so $p_{\alpha_1,\alpha_2}^+(z) = q_{\alpha_1}(z)$ for all $z \in \Theta$. Therefore,

$$p_{n,i}^* - q_1(z_i) \;\leq\; q_{\alpha_1}(z_i) - q_1(z_i), \tag{7.30}$$

for all $z_i \in \Theta$, with high probability.

Note that $q_{\Theta,\beta',m}(z) = q_{\beta'}(z)$ for all $z \in \Theta_m$. By Theorem 3.2 for all $z_i \in \Theta_m$

$$p_{n,i}^* - q_1(z_i) \;\geq\; q_{\beta'}(z_i) - q_1(z_i) \tag{7.31}$$

with high probability. Inequalities (7.30) and (7.31) imply that, for all $z_i \in \Theta_m$,

$$\left|p_{n,i}^* - q_1(z_i)\right| \;\leq\; q_\alpha(z_i) - q_{\beta'}(z_i)$$

with high probability. As in the proof of Lemma 5.2

$$\frac{\partial q_\alpha(z)}{\partial \alpha} \;\leq\; \frac{-e(z)}{\alpha e(z) + f(\rho(z)q_\alpha(z)}.$$

Hence,

$$q_{\alpha_1}(z) - q_{\beta'}(z) \;\le\; \int_{\alpha_1}^{\beta'} \frac{e(z)\,du}{ue(z) + f(\rho(z)q_u(z))} \;\le\; \alpha_1^{-1}(\beta' - \alpha_1).$$

□

Proof of Corollary 3.4. The corollary follows from Corollary 3.3, with appropriate choices of $\alpha_1, \alpha_2, \beta$ and β'. First note that $r_n^{1-\gamma_1}\phi_n \le c_1 r_n^{\gamma_1}/4$ for all n sufficiently large, if $r_n^{1-2\gamma_1}\phi_n \to 0$. Thus we can take $1 - \alpha_2 = \eta_{\Omega_n}$, $1 - \alpha_1 = r_n^{1-\gamma_1}\phi_n$ and $\beta' - \beta = \beta - 1 = r_n^{1-\gamma_1}\phi_n$, and satisfy $\alpha_1 \ge \alpha_2$ and $\beta' - 1 \le \eta_{\Omega_n}/2$ for all n sufficiently large. With these choices of α_1 and α_2, inequality (3.2) of Theorem 3.1 holds for all n sufficiently large; the choices of β and β' show that inequality (3.5) holds, fulfilling the conditions of Theorem 3.2. Then the probabilities in Corollary 3.3 converge to 1, as required, in view of (3.6) and (3.4), and $\alpha_1^{-1}(\beta' - \alpha_1) = O(r_n\phi_n)$ and $m \asymp \phi_n$. □

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